Dynamics of dominant tree species in a forest ecotone on the northern slop of Changbai Mountain

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Abstract: The competition and dynamics of dominant trees species in the forest ecotone between the broad-leaved/Korean pine (*Pinus koraiensis*) mixed forest and the spruce-fir forest（also known as dark conifer forest）in Changbai Mountain，Jilin Province in Northeast China were studied by using Lotka-Volterra model, based on the data from twenty-eight sample plots with area of 20 m×90 m for each one. Results showed that under natural condition, differentiation of communities followed two directions: one would be Spruce (*Picea jezoensis* and few *P. koraiensis*) and fir (*Abies nephrolepis*) co-dominant conifer forest, and at the equilibrium fir was absolutely preponderant (77.1% of relative dominance (RD)); the other would be the conifer and broad-leaved mixed forest, and at equilibrium, the broad-leaved tree species was 50% of RD in the broad-leaved/Korean pine mixed forest and 66% of RD in the broad-leaved and spruce-fir mixed forest. The study demonstrated that both broad-leaved/Korean pine mixed forest and dark conifer forest were climax community, the ecotone had transitional characteristics, and the diversification of the forest communities suggested that the direction of succession was affected by local habitat.

Keywords: Competition and dynamics; Lotka-Volterra model; Forest ecotone; Changbai Mountain

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Introduction

Resource availability limits plant population growth (e.g. Zhang 2003). Under resource limitation, biological factors provide a greater influence on population size than climatic factors (Wang *et al.* 1987). Population survival is often controlled by intraspecific and interspecific competition (Liu *et al.* 1998; Wu *et al.* 2001). According to the definition by Krebs (1994), competition occurs when two species use the same resource or harm each other when seeking resource. Competition also occurs among individuals or groups within species, often more furiously, because they use the very same resources. Therefore, ecologists have long thought that both interspecific and intraspecific competitions are pervasive in nature (Filho *et al.* 2005), and they play an important role in the process of vegetation dynamics (Song *et al.* 2000). Studies on the interaction of species may be helpful to understand the community development and succession.

Plant species in the forest ecotone display some intricate intraspecific and interspecific relationships in the north slope of Changbai Mountain, due to the abundant species and complex community composition. In some areas within the forest ecotone, there was not only historical disturbance, but also some present anthropogenic activities, such as the deforestation for construction of communication and power lines in the area. As a result, some pioneer tree species have been favored in this area, which may mislead us for the identification of the forest community types and the transitional characters. Therefore, further investigation on vegetation structure and composition may give us an insight into the processes determining population dynamics over time. Furthermore, studies on the forest ecotones in Changbai Mountain were almost absent (Zou *et al.* 2001).

The objective of this study is to explore the forest dynamics in the forest ecotones through a study on inter- and intra-specific competition, analysis of the dynamics of dominant tree species, and prediction of the succession trends of communities.

Material and methods

Study site

This study was carried out on the north slope of Changbai Mountain (41°31′–42°28′N, 127°9′–128°55′E) in Northeast China. There are four vegetation zones arranged with elevation from 700 m to 2691 m asl (above sea level). An altitudinal ecotone (1050−1250 m a.s.l.) (Yu *et al.* 2004) was selected between the broad-leaved/Korean pine mixed forest and the spruce-fir forest (also known as dark conifer forest) as our study site. Communities in the ecotone are composed of all the dominant trees in two adjacent communities, including coniferous trees, such as Korean pine (*Pinus koraiensis*), fir (*Abies nephrolepis*), larch (*Larix olgensis*), spruce (*Picea jezoensis*), and deciduous broad-leaved trees, such as *Betula platyphulla*, *Quercus mongolica*, *Acer ukurunduense*, *Populus davidiana*, *Fraxinus mandshurica* and *Tilia amurensis*. At the study area, mean annual precipitation is approximately 782.4 mm, mean annual temperature is 0.9 °C.

We selected 28 sample plots with area of 20 m×90 m for each one in 10 elevation gradients (3 plots in each elevation

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other than 1 050 m (only 1 plot)) in the ecotone (Table 1). In each plot, tree species, diameter at breast height (DBH), tree height were measured, and every tree with DBH≥2.5cm in the plots was recorded.

Table 1. Characters of sample plots

Elevations (m)	No. of plots	No. of tree species	Proportion of conifer tree species (Relative dominance, %)
1050	1	11	65.85
1100	3	16	66.07
1120	3	9	70.4
1150	3	10	71.27
1170	3	16	80.27
1190	3	18	84.44
1200	3	12	92.39
1210	3	15	95.16
1230	3	9	93.43
1250	3	7	91.54

Competition analysis

The Lotka-Volterra (LV) model for vegetation competition and dynamics analysis was applied in this study. The LV model was proposed independently by Lotka (1925) and Volterra (1926) in Italy, and has been universally used to analyze and predict dynamics of ecosystem. The LV competition model is often written as follows:

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i + \sum_{i=1}^{n} a_{ij} N_j}{K_i}\right) \quad (1)$$

where, $i, j = 1, 2, \ldots n$ ($i \neq j$), K_i is the carrying capacity of species i in absence of any other species, r_i the instantaneous increase rate of species i, a_{ij} the competition coefficient of species i to species j, N_i the population amount of species i, K_i and N_i in initial definition are population density. However, the density is influenced by individual size and may not reflect the status and effect of the dominant trees clearly in community. Consequently it is objective to substitute relative dominance (RD) for density (Song *et al.* 2000; Wu *et al.* 2001; Chen *et al.* 2004). a_{ij} is often calculated by the niche overlap equation as follows (May *et al.* 1972; Pianka 1974; Yang *et al.* 1992).

$$a_{ij} = \sum_{k=1}^{n} (P_{ik} P_{jk}) / \sum_{k=1}^{n} P_{ik}^2 \quad (2)$$

where, P_{ik} and P_{jk} represent the relative dominances (RD) of species i and j in the kth stand, respectively. In this paper, P is the ratio of sum of basal area (1.3 m) for a group of a certain tree species (DBH > 2.5 cm) to sum of all tree (DBH > 2.5 cm) species' basal area. In some other papers, P is the relative important value (RIV). We substituted RD for RIV, because individual amount of fir and spruce was often large, but the average DBH was small, which might place an excessive effect on RIV and then on competition coefficient a_{ij} (Chen *et al.* 2004).

LV model predicts that, under relatively stable environmental conditions (i.e. when there is a lack of disturbance or stress), coexistence of species with similar requirements occurs when intraspecific competition is more intense than interspecific competition (Goldberg and Barton 1992; Kokkoris *et al.* 1999; Aguiar *et al.* 2001). Theoretically, model prediction of two species competition gives three results. In general, it will be depended on the following competition coefficient a_{ij} and carrying capacity K_{ij} value, LV model predicts three possible outcomes when two species are competitive with each other:

1) When $a_{12}>K_1/K_2$ and $a_{21}<K_1/K_2$, implies species 1 excludes species 2;

2) When $a_{21}>K_2/K_1$ and $a_{12}<K_1/K_2$, implies species 2 excludes species 1;

3) When $a_{12}<K_1/K_2$ and $a_{21}<K_2/K_1$, implies coexistence.

Results and discussion

Population relative dominance

The study on species structure and composition showed that the dominant tree species in the overstory in the ecotone were fir (25.7% of RD), larch (14.7% of RD), spruce (17.0% of RD) and Korean pine (23.3% of RD). Due to relative lower proportion, large number, complex and variable composition and wide niche (Zhu 1993) of broad-leaved species, all broadleaf tree species were integrated into one group called broad-leaved tree species for statistic analysis. Few *Picea koraiensis* (<3% of RD), considering their similar biological characters to the *Picea jezoensis*, was grouped into spruce (*Picea spp.*).

Elevation and mean RD of 5 dominant tree species in 28 sample plots are given in Table 1 and Fig. 1. With increasing altitude, RD of broad-leaved tree species and Korean pine declined, while RD of fir, spruce and larch increased. However, the extents of decline and increase were not significant, which may be a reflection of gradual variation in the ecotone along the elevation.

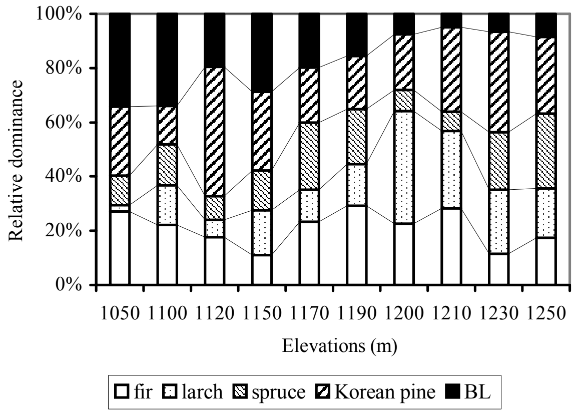

Fig.1 Mean relative dominance of dominant tree species in the ecotone between the broad-leaved/ Korean pine mixed forest and spruce-fir forest. * BL stands for broad-leaved tree species, respectively

Population competition coefficient (*a*)

According to RD of 5 dominant species in 28 plots, competition coefficients (a_{ij}) among dominant species were calculated and are given in Table 2. It shows the competition coefficients between fir, spruce, and broad-leaved tree species, as well as between each of them and the rest tree species are more than 0.6, indicating the three species have very similar requirement for the habitat and severe competition.

Table 2. Competition coefficient among dominant tree species (a_{ij})

Tree species		Tree species				
		1	2	3	4	5
		Abies nephrolepis	*Larix olgensis*	*Picea spp.*	*Pinus koraiensis*	Broad-leaved trees
1	*Abies nephrolepis*	1	0.8462	0.6732	1.0838	0.6751
2	*Larix olgensis*	0.6205	1	0.4531	0.8823	0.3498
3	*Picea spp.*	0.8842	0.8116	1	1.2944	0.6561
4	*Pinus koraiensis*	0.4326	0.4802	0.3933	1	0.4794
5	Broad-leaved trees	0.8911	0.6295	0.6592	0.6240	1

High competition coefficients were found between Korean pine and any other tree species, especially with fir, spruce, where competition coefficients (a_{14}, a_{34}) were over 1. The result suggested that Korean pine has been strongly influenced by other tree species. In the ecotone, there was an intensive competition among dominant trees species from two adjacent communities, especially among three conifer tree species: spruce, fir and Korean pine. The results from a_{14}>1 and a_{34}>1 suggested that Korean pine was hard to survive in the spruce and fir-dominated communities. However, the outcome from a_{41}<0.5 and a_{43}<0.5 suggested that spruce and fir could survive well in the Korean pine-dominated community. In addition to Korean pine, larch also had a larger competition coefficient with fir, suggestive that existence of larch had an inhibiting effect on fir growth. In addition to Korean pine, other tree species also had a large competition coefficient with larch, indicating that their existence had an obvious effect on larch growth. The above results demonstrated the species biological feature: similar to r-strategy species in succession process (Shen *et al.* 2001; Luo *et al.* 2002), large number of fir presented in the community. While Korean pine was a K-strategy species, its individual number was small. Therefore, in spruce and fir-dominated community, understory light intensity was very low, and regeneration and growth of shade-intolerant Korean pine and broad-leaved tree species were obviously suppressed. On the contrary, in Korean pine dominated community, canopy density was low, and spruce, fir and broad-leaved tree species could grow well. Since spruce, larch and Korean pine were taller than fir, the larger competition coefficients between them indicated they had a common demand for spatial habitat.

Carrying capacity of species (*K*)

There are often two methods to estimate *K* value: one is taking the dominance in its pure stand as *K* value (Wang 1984; Wu *et al.* 2001); the other is taking the mean dominance of tree species in its absolutely prominent stands as *K* (Song *et al.* 2000). Both methods have achieved good results. Our study took the mean dominance of each species in its prominent 8 plots of the total 28 plots as respective *K* value. The result showed that *K* values of fir, larch, spruce, Korean pine and broad-leaved tree species were 16.34, 20.61, 16.02, and 28.38, 22.71 $m^2 \cdot hm^{-2}$, respectively.

Competition determination

According to the *K* values of dominant tree species, *K* value ratio was evaluated by using LV competition equation (Table 3). According to the Table 2 and Table 3, we could determine:

Table 3. Ratios of *K* value between the dominant tree species （K_i/K_j）

Tree species	Tree species				
	Abies nephrolepis	*Larix olgensis*	*Picea* spp.	*Pinus koraiensis*	Broad-leaved trees
Abies nephrolepis	1	0.7928	1.0198	0.5757	0.7193
Larix olgensis	1.2614	1	1.2864	0.7262	0.9074
Picea spp.	0.9806	0.7774	1	0.5645	0.7054
Pinus koraiensis	1.7371	1.3771	1.7714	1	1.2495
Broad-leaved trees	1.3902	1.1021	1.4177	0.8003	1

1) Because of $a_{12}>K_1/K_2$ and $a_{21}<K_2/K_1$, $a_{14}>K_1/K_4$, and $a_{41}<K_4/K_1$, fir would finally win when competing with larch or Korean pine population. Fir is a shade-tolerant tree species that can survive and grow under relative dense stand and develop quickly with improved light condition. When one or more big trees fall to form a gap and the forest floor is exposed to high light, fir regeneration and growth will be promoted. Therefore, fir is not only the principal component of the overstory, but also a dominant component of the understory regeneration. On the contrary, only a few Korean pine seedlings and saplings can establish and survive in forest floor. Because of its slow early growth (Xu *et al.* 1983) and weak adaptation to light variation (Yao *et al.* 1983), Korean pines can not quickly occupy the growing space when the gap is formed. Consequently, Korean pine sapling is rare in the forest. Larch and broad-leaved trees are shade intolerant species. When they are exposed to the full light condition in a big gap, they may quickly occupy the space. These species, however, because of short life span, will be eventually replaced by shade-tolerant tree species (such as fir).

2) Because of $a_{23}<K_2/K_3$, $a_{32}>K_3/K_2$ and $a_{34}>K_3/K_4$, $a_{43}<K_4/K_3$, spruce would finally win when competing with larch or Korean pine population. Spruce has a similar biological feature to fir. Therefore, it will eventually exclude larch and Korean pine population.

3) Because of $a_{13}<K_1/K_3$, $a_{31}<K_3/K_1$; $a_{15}<K_1/K_5$, $a_{51}<K_5/K_1$; $a_{24}<K_2/K_4$, $a_{42}<K_4/K_2$; $a_{35}<K_3/K_5$, $a_{53}<K_5/K_3$ and $a_{45}<K_4/K_5$, $a_{54}<K_5/K_4$, coexistence would be expected between fir and spruce, fir and broad-leaved tree species, larch and Korean pine, spruce and broad-leaved tree species. Because of lower density and thus better light condition in Korean pine-dominant community, spruce, broad-leaved tree species and larch can finish their life cycle. Similarly, broad-leaved tree species-, larch- and

spruce-dominated forests often have lower density than fir-dominated forests, and sunlight condition near the forest floor can meet the demand for spruce regeneration and growth.

According to the discussion above, in the ecotone between the broad-leaved/Korean pine mixed forest and spruce-fir forest, the community could develop following two directions: one was towards spruce-fir forest community; other was towards a deciduous broadleaved and conifer mixed forest community, dominated by Korean pine, or spruce-fir and some broad-leaved tree species.

According to LV model, natural population growth is stopped and community reaches the balance when $t \to \infty$, $dN_i/dt = 0$, that is, $N_i + \sum a_{ij}N_j = K_i$, and then $\sum N_i > \max K_i$ because of utilizing overlap resources (e.g. Wu *et al.* 2001; Chen *et al.* 2004). In the spruce / fir community, dominance of fir (N_1) was 13.72 $m^2 \cdot hm^{-2}$, 77.1% of RD, and spruce (N_3) was 4.08 m^2/hm^2, 23.9% of RD. At the same time, $N_1 + N_3 = 17.8$ $m^2/hm^2 > K_i$ (i = 1, 3). In the broad-leaved/Korean pine community, dominance of Korean pine (N_4) was 17.24 $m^2 \cdot hm^{-2}$, 49.0% of RD, and broad-leaved tree species (N_5) was 17.91 $m^2 \cdot hm^{-2}$, 51.0% of RD. At the same time, $N_4 + N_5 = 35.12$ $m^2 \cdot hm^{-2} > K_i$ (i = 4, 5). In the broad-leaved and spruce-fir community, dominance of spruce (N_3) was 2.31 $m^2 \cdot hm^{-2}$, 10.2% of RD, fir (N_1) was 5.33 $m^2 \cdot hm^{-2}$, 23.4% of RD, and broad-leaved tree species (N_5) was 15.80 $m^2 \cdot hm^{-2}$, 66.4% of RD. At the same time, $N_1 + N_3 + N_5 = 23.44$ $m^2 \cdot hm^{-2} > K_i$ (i = 1, 3, 5).

Prediction of dominant tree species competition in the three communities showed that the sum of dominance for the dominant tree species was larger than carrying capacity of each tree species. It implied that the 3 co-dominant communities could sufficiently exploit environmental resource by their niche overlaps. At the same time, dominance of the 5 dominant tree species in the 3 co-dominant communities suggested that total dominance in spruce and fir- dominated community was smaller (17.8, 23.44 $m^2 \cdot hm^{-2}$, respectively) than that in Korean pine-dominated community (35.12 $m^2 \cdot hm^{-2}$). Spruce and fir dominated in a community mainly through their high density, not through their large size, especially fir. In all sample plots, fir (DBH $\geq$ 2.5cm) had up to 296 stems per plot, and spruce (DBH $\geq$ 2.5cm) had up to 163 stems per plot. However, their average DBH were less than 20 cm. These two tree species suppressed the existence of other tree species through its dense distribution in the habitat, either by occupying overstory and understory to form the spruce and fir-dominated community, or by occupying overstory in a few individuals and understory in a large number of individuals to form spruce-fir and broad-leaved tree species forest. On the other hand, Korean pine dominated in community mainly through its large size. In all sampled plots, Korean pine (DBH $\geq$ 2.5cm) had less than 50 stems per plots, but their average DBH was about 50 cm and most of them occupied overstory. Different composition and structure of communities indicated the difference in species survival strategy.

At the equilibrium, the community composition and structure in the ecotone under natural condition was similar to those in two adjacent communities, which indicated that the broad-leaved/Korean pine mixed forest and the spruce-fir forest were both climax communities in different altitudinal gradient in Changbai Mountain. At the same time, differentiation of communities in ecotone further indicated the transitional characters of the ecotone. Considering that soil and topography in the ecotone are relative homogenous, the principal factors controlling community differentiation would likely be climatic factors. Therefore, the ecotone community would differentiate to the adjacent community types. That is to say, along altitudinal gradient, the community near the low elevation would develop similarly to broad/leaved Korean pine mixed forest, and the community near the high elevation would develop similarly to spruce-fir forest. However, forest communities sampled in the study displayed a mosaic distribution, depending on local site conditions. The elevation of the ecotone was only ranged from 1050 m to 1250 m (Yu *et al.* 2004), and there was little difference in climatic factors. Composition and structure of community in the ecotone depended on inter- and intra-species competition. The final winner of the species competition depended on the local site condition.

Conclusions

In the ecotone between the broad-leaved/Korean pine mixed forest and spruce-fir forest, naturally differentiation of community occurred in two directions: one was towards spruce and fir-dominated conifer forest; the other was towards the broad-leaved and conifer mixed forest, which was composed of Korean pine or spruce-fir and broad-leaved tree species. Our study demonstrated that i) the broad-leaved/Korean-pine forest and the dark conifer forest appeared as the steady climax communities; ii) the differentiation trends indicated some obvious transition characteristics of community in the ecotone; iii) diversification of community types suggested that the direction of succession was affected by site conditions.

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